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THE AFFINITIES OF THE OPHIOGLOSSACEÆ AND MARSILIACEÆ.

DOUGLAS H. CAMPBELL.

The last ten years have been notable for many important contributions to our knowledge of the pteridophytes, due in part to a more exact investigation of many forms already studied, but still more to a critical study of tropical types, which hitherto have been studied more or less superficially, owing to the difficulty of procuring suitable materials for complete investigations. The fossil forms have also yielded much important material for a better understanding of the affinities of some of the living ones.

The work has covered a wide field and comprises very valuable additions to our knowledge of the anatomy and development of many interesting types which were but imperfectly known before. These investigations have added materially to the data available for a critical comparison of the different groups, and we are in a much better position than ever before to understand the affinities of some of the more puzzling types of pteridophytes. It must be admitted, however, that the conclusions of botanists in regard to the relationships of certain groups are by no means entirely in accord.

There are two orders of ferns about whose relationships there has been a good deal of controversy, and it is the bearing of some of the recent investigations upon these relationships to which the writer would direct attention. The two orders referred to are the Ophioglossaceæ and the Hydropteridineæ, especially the Marsiliaceæ.

THE OPHIOGLOSSACEÆ.

The Ophioglossaceæ constitute a very natural family of fern-like plants, evidently closely related among themselves, but whose affinities to the other pteridophytes have been much discussed. They are generally considered to belong to the Filicineæ, or ferns with which they agree in their general structure. The writer has expressed the opinion that the sporangium of Ophioglossum represents the lowest type found in the fern series. This conclusion is based upon the structure of the living forms, as the Ophioglossaceæ are almost unknown in a fossil condition, perhaps owing to the soft tissues which characterize them. These would hardly be preserved as fossils except under the most favorable conditions.

As is well known, the Ophioglossaceæ differ from the typical ferns in the position of the sporangia, which are borne upon a peculiar structure (sporangiophore) arising from the inner surface of the leaf, either directly from the lamina or from the petiole. The sporangiophore may be a simple spike with two rows of large sporangia scarcely projecting at all, or it may be much branched and the numerous sporangia quite distinct and even stalked. (Campbell, *Mosses and Ferns*, p. 296.) The former structure occurs in Ophioglossum, the latter in Botrychium and Helminthostachys. The simpler species of Botrychium, such as *Botrychium simplex* and *Botrychium lunaria*, form a transition between the type of Ophioglossum and the larger species of Botrychium and Helminthostachys, in which both the sterile and fertile leaf segments are much branched, and the free sporangia bear a certain resemblance to those of Osmunda or Angiopteris. It is possible that the latter types, or at any rate Osmunda, may have arisen from forms like Botrychium or Helminthostachys, through which they would be connected with the more primitive type of sporangium found in Ophioglossum.

Much the most important recent work upon the sporangia of these puzzling forms is that of Bower ("Studies in the Morphology of Spore-Producing Members"; *Phil. Trans.*, 1894–1903, 185–196), whose views as to the relationship of the Ophioglossaceæ differ radically from those of most students of the pteridophytes. He considers the whole spike of Ophioglossum as the equivalent of a single sporangium of Lycopodium, produced by growth and septation from an originally unilocular structure. He is not inclined to admit any direct relationship between the Ophioglossaceæ and the true ferns, and thinks they are probably more nearly related — although very remotely — to the lycopods. In his most recent work (*loc. cit.* No. V, p. 253), however, he recognizes the importance of the decidedly fern-like character of the gametophyte and recedes somewhat from the extreme views expressed in the earlier paper. He seems still unwilling, however, to give up the homology between the sporophyll in Ophioglossum and Lycopodium. It is held that all the pteridophytes are reducible to a common strobiloid type, which is most clearly seen in the lycopods and Equisetaceæ, but which is believed to be recognizable in the ferns as well. With this view the writer has been unable to agree.

Bower thinks it inconceivable that a large-leaved type could originate directly from any conceivable form of bryophyte sporogonium, and therefore concludes that all the primitive pteridophytes must have been microphyllous. To the writer there seems to be no greater difficulty in assuming that a single leaf-like organ may have been developed at the base of the sporogonium (*Mosses and Ferns*, p. 515) than that a series of small leaves should be developed as eruptions from its surface. Why both forms may not have been developed quite independently is not clear, either from the evidence of comparative morphology, or from the fossil record. That a special assimilative structure, remotely comparable to a leaf, may originate from the base of the sporogonium is shown in many mosses, where the apophysis is of this nature. In certain species of Splachnum the apophysis assumes a relatively very large size, and is expanded into a disc which might almost be compared to a perfoliate leaf. Of course there is no question of a direct homology between the apophysis of a moss and the leaf of a vascular plant, but the fact is patent that the sporogonium of a moss may give rise to a special assimilating organ, and it is therefore quite conceivable that the progenitor of the large-leaved ferns may have arisen from some bryophytic type by an analogous formation of a special organ which became a true leaf subtending a sporogenous structure much as is actually seen in Ophioglossum.

That the Ophioglossaceæ represent an ascending series, as Professor Bower (Bower, *loc. cit.* No. 5, p. 233) believes, is extremely probable; but that the lowest members of the series are to be connected with forms in any way like the Lycopodiaceæ appears to the writer exceedingly doubtful. The direct origin of a type like Ophioglossum from an Anthoceros-like prototype has been considered at length elsewhere (Campbell, — *loc. cit.*, p. 515) and will not be discussed further here.[1]

The numerous structural resemblances in both gametophyte and sporophyte between the Ophioglossaceæ and Marattiaceæ are too great to be passed over, and indicate a genuine relationship between the two. It seems to the writer that the importance of these obvious resemblances has been rather minimized by some recent authors, and it may be just as well to call attention afresh to some of the most striking ones.

Our knowledge of the gametophyte of the Ophioglossaceæ is now pretty complete, owing to the important researches of Jeffrey (The Gametophyte of Botrychium virginianum, *Proc. Canad. Inst.* V, 1898) and Lang (On the prothalli of Ophioglossum pendulum and Helminthostachys zeylanica, *Ann. Bot.* 16, 1902). The former has described in detail the prothallium of *Botrychium virginianum*, while Lang was fortunate enough to procure fairly complete material of *Ophioglossum pendulum* and *Helminthostachys zeylanica*, so that all three genera are represented. As might be expected, there is a good deal of similarity, this being most marked between Botrychium and Helminthostachys. All agree in having a subterranean prothallium which is destitute of chlorophyll, thus resembling the prothallia of certain species of Lycopodium. It is highly improbable that this condition is a primitive one, however, and too much stress cannot be laid upon it in making a comparison with the green prothallia of the Marattiaceæ, with which otherwise there is a close agreement, especially in the case of Ophioglossum. As some species of Lycopodium have a green prothallium, and chlorophyll has been found under certain circumstances in the prothallium of Ophioglossum (Mettenius — *Filices Hort. Bot. Lips*, 1856), it is extremely likely that the absence of chlorophyll is a secondary condition, and that so far as the prothallium is concerned, the Marattiaceæ approach more nearly the ancestral type than do the Ophioglossaceæ.

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[1] Since this paper was written there has been published by Bower (*Ann. of Bot.* Apr. 1904) an account of a remarkable species of Ophioglossum from Sumatra, in which the leaf consists simply of a long-stalked sporangiophore with scarcely a trace of the sterile segment. This interesting plant almost realizes the hypothetical form assumed by the writer as the ancestor of the ferns.

Both Jeffrey and Lang are agreed as to the essentially fern-like character of the prothallium. This is shown in its apical growth, strongly dorsiventral form, and especially in the reproductive organs, which in Ophioglossum (Fig. 1, *A*, *B*) resemble to an extraordinary degree those of Marattia. The large multiciliate spermatozoids are also entirely fern-like in form. When to the close resemblance in the sexual organs is added the marked correspondence in the development of the embryo, which is very similar to that of the Marattiaceæ and not in the least like that of Lycopodium, the case seems a very strong one.

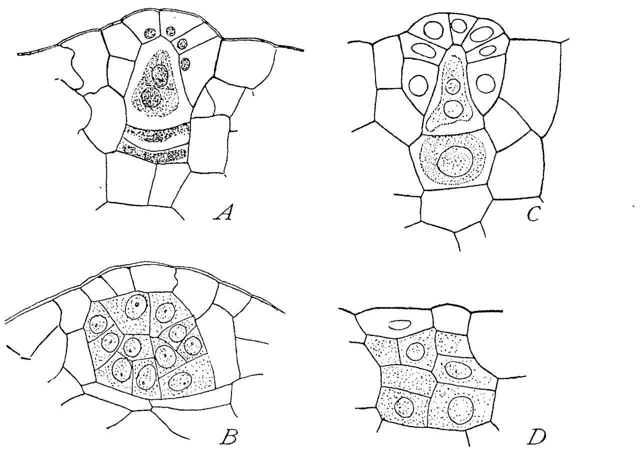

FIG. 1.—*A*, archegonium; *B*, young antheridium of *Marattia douglasii*, × 350. *C*, archegonium; *D*, young antheridium of *Ophioglossum pendulum*, × 250. *C*, *D*, after Lang.

There next remains to be considered the structure of the adult sporophyte. In most species of both Ophioglossum and Botrychium the stem is a short upright rhizome about which the leaves are spirally arranged. In *Ophioglossum pendulum*, however, and in Helminthostachys the plant is dorsiventral. Among the Marattiaceæ both types also occur. Marattia and Angiopteris are radial, Danæa is dorsiventral. Bower (*loc. cit.*,

p. 219) is inclined to consider the radial type as older than the dorsiventral, but as both types occur in both families under consideration, this has little bearing upon the question of their relationships.

In the structure of the apical meristems the Ophioglossaceæ are even more fern-like than the Marattiaceæ, as they regularly show a single tetrahedral initial in both stem and root. In this respect they resemble the leptosporangiate ferns more than they do the Marattiaceæ. In the very young sporophyte of the latter, however, the root shows a single apical cell which is replaced by a group of initials in the more massive roots of the older sporophyte.

The very complicated vascular system of the older sporophyte in the Marattiaceæ is undoubtedly associated with the massive stem. A study of the young plant shows that in the earlier stages there is a single cylindrical stele much like that which occurs in the adult rhizome of Helminthostachys and such leptosporangiate ferns as Gleichenia. This is considered by Jeffrey to be a primitive condition from which the more complicated arrangement found in the adult stem of the Marattiaceæ has been derived. The arrangement of the vascular bundles in the stem of Ophioglossum is much like that in the typical ferns, while Botrychium closely resembles Osmunda. (Jeffrey, "Structure of the Stem in the Pteridophyta and Gymnosperms," *Phil. Trans.* 195, 1902.)

The leaves of the Ophioglossaceæ, which are in some respects different from those of the typical ferns, nevertheless are much more like these than like either the lycopods or Equisetaceæ. The venation is not essentially different from that of the Marattiaceæ, and although there is never found the circinate form of the young leaf, so characteristic of the ferns, still in the larger species of Botrychium there is an approach to this which suggests that the coiling of the young leaf is connected with the very great development of the lamina of the leaf which characterize most ferns.

While the reticulate venation found in Ophioglossum is different from that in most ferns, still there are many ferns which show a very similar venation. Thus among the Marattiaceæ there may be instanced Kaulfussia, whose venation is not very different from that of Ophioglossum, and possibly a further comparison might be made in the form of the leaf with the palmately lobed leaf of *Ophioglossum palmatum.* On the other hand, the venation of Agiopteris or Danæa is almost identical with that of Helminthostachys. (See Fig. 2.)

Farmer (Farmer & Freeman, "The Structure and Affinities of Helminthostachys," *Ann. Bot.* 1899) has referred to the stipules of the latter genus and thinks they are not directly comparable to those of the Ophioglossaceæ, although it is not quite clear wherein the difference consists. There certainly seems to be no essential difference between the stipular structure at the leaf base in Botrychium (Campbell, *Mosses and Ferns*, p. 242) and those in Marattia or Danæa, although in the latter genera the stipules are more distinct. The development of stipular structures is especially marked in both Ophioglossaceæ and Marattiaceæ, while among the Leptosporangiatæ they are generally absent except in the Osmundaceæ, which are admittedly the nearest relatives among the Leptosporangiatæ to the eusporangiate ferns.

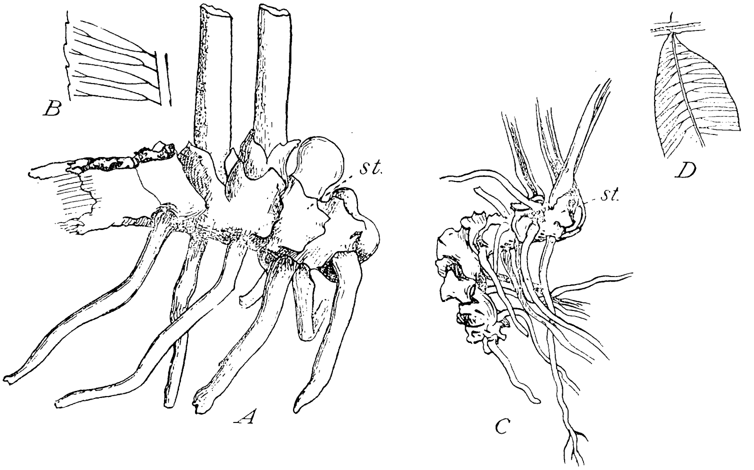

FIG. 2.—*A*, rhizome of *Helminthostachys zeylanica*, after Farmer; *B*, part of a leaflet of the same plant, showing the venation; after Hooker & Baker: *C*, Rhizome of *Danæa alata*, (reduced); *D*, base of leaflet showing venation; st., stipules.

The markedly dorsiventral rhizome of Danæa is strongly suggestive of that of Helminthostachys (Fig. 2, *A*, *C*), and the position of the leaves and roots is much the same. The cylindrical stelar tube with relatively small foliar lacunæ in Helminthostachys may perhaps be compared to the stele in the young rhizome of Danæa, which, according to Jeffrey, is of much the same type. (Jeffrey, *loc. cit.*, pp. 120, 121.)

The most marked histological difference between the Marattiaceæ and the Ophioglossaceæ is perhaps the occurrence of conspicuous mucilage ducts in the former. These are, however, also wanting in the other ferns. The circinate form of the young leaves is probably associated with the great development of the lamina of the leaf, but is certainly a difference of some importance.

To the labors of Bower we owe by far the most important contributions to our knowledge of the development of the sporangium that have been made for many years. These enable us to make a detailed comparison of all the developmental stages in each group, and a careful study of his descriptions and figures of the two groups in question have led me to a somewhat different result from that reached by him.

The progression from the sporangial spike of Ophioglossum to the much branched sporangiophore of Botrychium or Helminthostachys, with its numerous distinct sporangia, is comprehensible enough; but the relation of the sporangiophore of the Ophioglossaceæ to the sporangia of the other pteridophytes is not so obvious. Bower believes (*loc. cit.*, p. 250) that all pteridophytes may be reduced to the strobiloid type, this being reduced to a single sporophyll in Ophioglossum. As we have stated elsewhere, this theory seems hardly satisfactory when applied to the ferns, however probable it may appear for the other pteridophytes. The comparison of the sporangial spike of Ophioglossum to the single sporangium of Lycopodium appears rather improbable, and it seems more in accordance with the facts to consider it an entirely distinct development, derived directly from the whole upper part of the sporogonium of the ancestral form.

Bower's very complete account of the sporangia in Ophioglossum and the Marattiaceæ suggests a possible point of contact between the two groups. In the very peculiar *Ophioglossum palmatum*, there may be several nearly sessile sporangiophores borne near, or actually upon, the margin of the large palmately lobed sterile segment of the leaf. Among the Marattiaceæ Danæa shows a marked resemblance to Ophioglossum in the arrangement of the loculi in the greatly elongated synangia, which almost completely cover the lower surface of the contracted sporophylls. A study of the development of the sporangia in the two, to judge from Bower's account and figures, shows a close resemblance in many particulars.

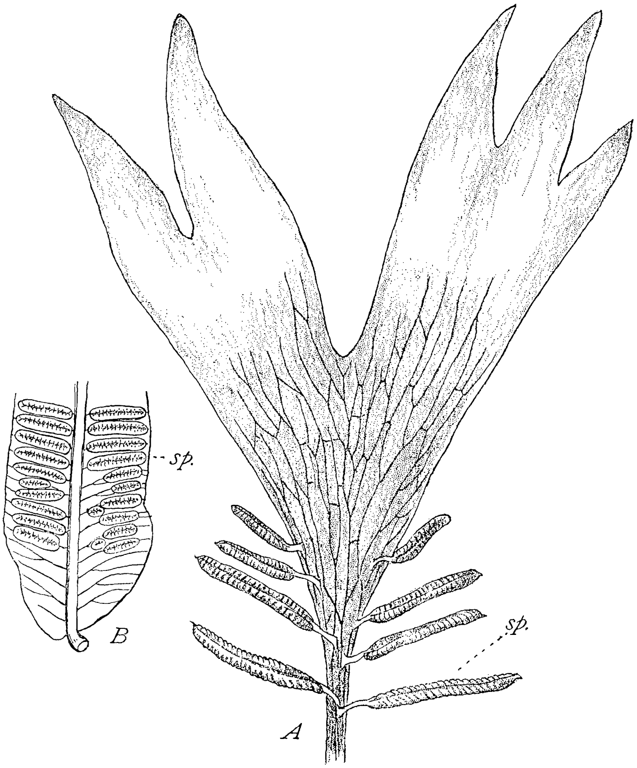

FIG. 3.—*A*, leaf of *Ophioglossum palmatum*, showing the position of the numerous sporangiophores, *sp.*, —after Bower; *B*, part of a sporophyll of *Danæa alata*, showing the elongated synangia, *sp.*; × 2.

Bower thinks that the elongated synangium of Danæa has been secondarily derived from a circular one, like that of Kaulfussia, but there is no certain evidence, either morphological or geological, that the type found in Danæa may not be the older. While a direct comparison of the sporangiophore of the existing species of Ophioglossum with the synangium of Danæa would be hardly justifiable, still it is conceivable that synangia of the type of Danæa might have originated from the complete adhesion to the surface of the sterile leaf segment of a series of small sporangiophores not so very different from those actually found in *Ophioglossum palmatum* (Fig. 3). If the primitive character of the synagium of Danæa is admitted, it is easy to trace the origin of the marattiaceous types by the expansion of the leaf lamina. Bower suggests that the primitive type of Marattiaceæ probably had an undivided leaf like that of *Danæa simplicifolia*, with scattered round sori similar to those of Kaulfussia. We agree with this except as to the character of the sori, which we believe were quite as probably like those of the actual *Danæa simplicifolia.*

In comparing the two families, Ophioglossaceæ and Marattiaceæ, it is clear that they closely resemble each other in the character of the reproductive organs and embryo, and also in the apical growth and dorsiventral form of the gametophyte. The position of the archegonia and the absence of chlorophyll are undoubtedly associated with the subterranean life of the gametophyte.

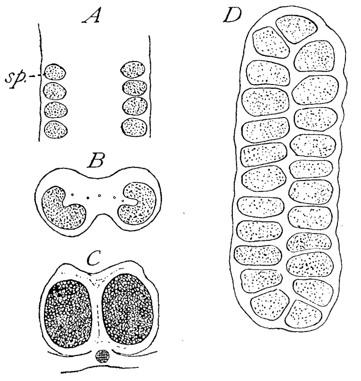

Fig. 4.— *A*, longitudinal section of part of the sporangiophore of *Ophioglossum pendulum*, × 2; *B*, cross-section of the same; *C*, cross-section of the synangium of *Danæa alata*, × 15; *D*, longitudinal section of the same.

While in the sporophyte such differences as the coiled vernation of the leaf, and presence of mucilage ducts in the Marattiaceæ must be taken into account, the two orders nevertheless agree in the general morphology of both stem and leaf, including the venation of the leaves, while in regard to the apical growth of the stem and root, the Ophioglossaceæ are more like the higher ferns than are the Marattiaceæ. Finally, whether or not the possibility of a direct connection between the two is admitted, there is no question of the strong resemblance between the sporangia of Ophioglossum and Danæa. In view of all these facts, we can see no valid reason for removing the Ophioglossaceæ from their association with the ferns, and we believe that their association with the Marattiaceæ among the eusporangiate ferns is entirely justified.

THE MARSILIACEÆ.

That the Marsiliaceæ are directly allied to some group of homosporous leptosporangiate ferns is apparent; but there has been little attempt to connect them directly to any of the existing ferns. The writer (*loc. cit.*, p. 421) has suggested a comparison with the peculiar Ceratopteris, and has also compared the antheridium with that of the Polypodiaceæ.

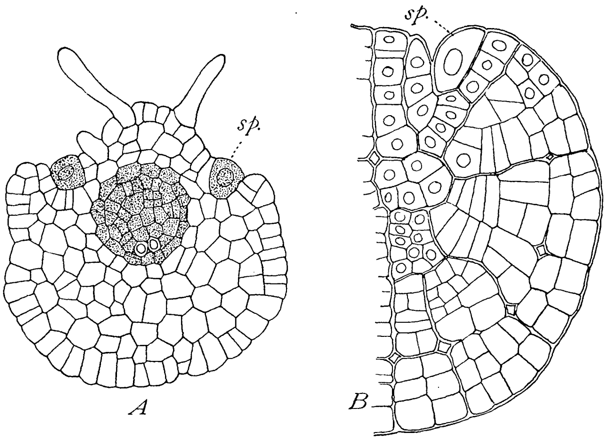

FIG. 5.—*A*, cross-section of a fertile leaf-segment of *Schizæa pennula*, highly magnified; *sp.*, sporangium mother-cell—after Prantl; *B*, cross-section of very young sporocarp of *Marsilia quadrifolia*, × 500, after Johnson. The marginal cell, *sp.*, gives rise to a row of sporangia.

The more recent work of Belajeff ("Die männlichen Prothallien der Wasserfarne," *Bot. Zeit.*, 1898) on the antheridium, and of Johnson ("On the leaf and sporocarp of Marsilia," *Ann. Bot.* XII, 1898) ("On the leaf and sporocarp of Pilularia," *Bot. Gaz.* XXVI, 1898) and Gœbel (*Organographie der Planzen*, Part II, 1900) upon the sporocarp, have suggested a somewhat different affinity, and it was thought worth while to look into the evidence carefully, supplementing it by a direct comparison of such material as was available.

Gœbel has called attention to the similarity between the young sporocarp of Marsilia and the fertile leaf-segment of Schizæa. Johnson's studies on the sporocarp of both Marsilia and Pilularia bear out this, and a comparison with Prantl's figures of the young sporophytes of Schizæa emphasizes the marked resemblance between the two (Fig. 5). Johnson does not admit the foliar nature of the sporocarp; that is, he does not believe the capsule is homologous with the leaf lamina, a view which has been expressed by the writer, and which is supported by most students of the subject. A comparison of the developing fertile segment of the leaf of Schizæa, however, shows that at the time the first rudiments of the marginal sporangia appear, there is no more trace of a lamina than in a corresponding stage of the sporocarp in Marsilia. In short, the structure of the very

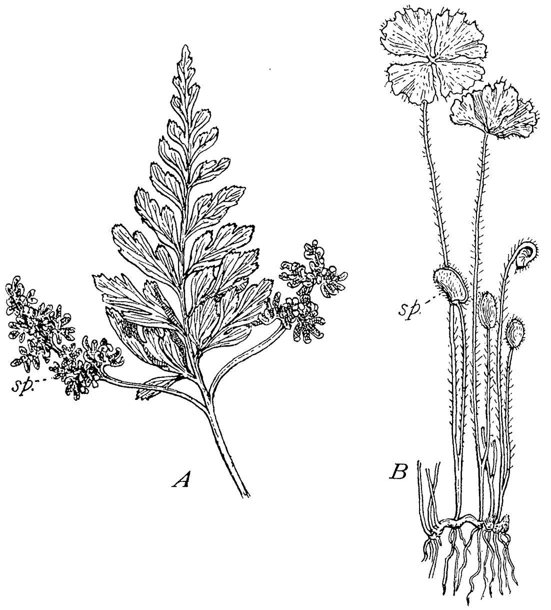

FIG. 6.—*A*, sporophyll of *Aneimia hirsuta*, showing the very conspicuous fertile pinnæ, *sp.*; *B*, Plant of *Mearsilia salvatrix*, with the long-stalked sporocarps, *sp.*, after Sachs.

young sporocarp of Marsilia and the fertile leaf segment of Schizæa is remarkably similar; moreover, the origin of the sporangia from originally marginal cells is noteworthy.

The origin of the sporocarps in the Marsiliaceæ, however, is different from that of the fertile leaf-segment in Schizæa, but finds a close counterpart in the allied genus Aneimia (Fig. 6) where the remarkably developed fertile pinnæ bear much the same relation to the rest of the leaf, that the sporocarp does in Marsilia. The pinnate form of the sporocarp in Marsilia and the dichotomous sterile segment, are comparable to what obtains

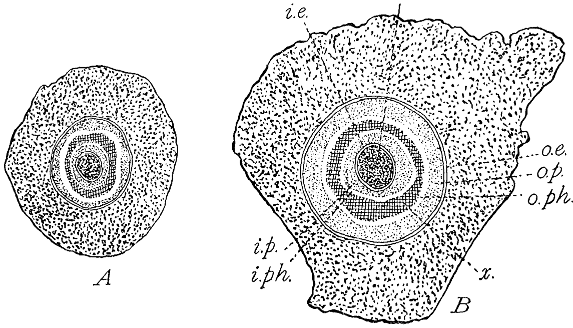

FIG. 7.—*A*, cross-section of the rhizome of *Marsilia vestita*, × about 15; *B*, similar section of the rhizome of *Aneimia hirsuta*. The outer cortical tissue is composed in both of brown sclerenchyma; the tubular stele encloses a medulla also composed of sclerenchyma; the stele has an outer (*o. e.*) and an inner (*i. e.*) endodermis, outer (*o. p.*) and inner (*i. p.*) pericycle; outer (*a. ph.*) and inner (*i. ph.*) phlœm; and a central xylem (*x*).

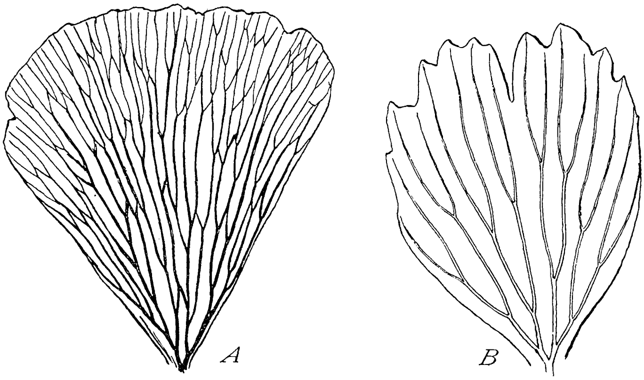

FIG. 8.—*A*, leaflet of *Nearsilia vestita*, × 10; *B*, pinnule of *Aneimia hirsuta*, × 8; both show a strictly dichotomous venation.

in some species of Schizæa, where the leaf is dichotomously divided, but the fertile segments are pinnate.

A comparison of the vegetative organs of the Marsiliaceæ and Schizæaceæ shows equally marked resemblances. The creeping rhizome of Marsilia and Pilularia is remarkably similar to that of Schizæa and certain species of Aneimia (Fig. 7), as may be clearly seen from the figure. The leaves also show interesting resemblances. Thus the filiform leaf of Pilularia finds its exact counterpart in the sterile leaves of *Schizæa pusilla*, while the four-lobed leaf of Marsilia is comparable to such species as *Schizæa pennula*, with dichotomously branched lamina. The venation in Schizæa and Aneimia is characteristically dichotomous, closely resembling that of Marsilia. Except in Lygodium, the pinnate venation found in the majority of the ferns does not occur among the Schizæaceæ.

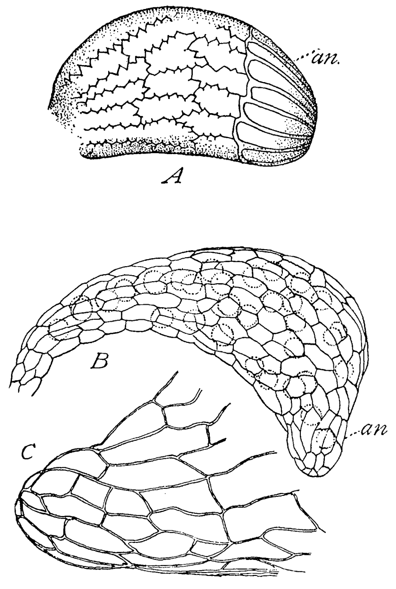

Fig. 9.—*A*, sporangium of *Schizæa pennula*, showing the apical annulus, *an*. × 45, (after Prantl), *B*, sporangium of *Pilularia Americana*; the apical region suggests the annulus of Schizæa; *C*, apical region, more enlarged.

So far as I am aware, no direct comparison of the sporangia in the two families has been made, although the early stages of the sporangium have been carefully studied. The Schizæaceæ differ from all the other ferns in the very peculiar form of the sporangium which is strongly oblique and has a terminal annulus. The sporangia of *Pilularia americana* and *Marsilia vestita* were examined, and it was found, especially in the case of the former, that the sporangia resembled strongly those of the Schizæaceæ. In Marsilia the closely packed microspore rendered it difficult to make out the form of the parietal cells, but in Pilularia the spores are widely separated and the form of the parietal cells is easily seen when the sporangia, after placing them in water for a short time, are treated with alcohol to check the swelling of the mucilaginous cell walls which otherwise are soon completely destroyed. The oblique form of the sporangium is especially conspicuous in Pilularia (Fig. 8, *B*), and the arrangement of the cells near the apex is very suggestive of the annulus of Schizæa, although of course in these aquatic plants, no hardening of the annulus cells takes place.

This remarkable correspondence in the structure of the sporangium, taken together with the other close structural resemblances, justifies the assumption of a not very remote relationship between the Schizæaceæ and Marsiliaceæ.

It may be added that this view would tend to confirm the contention of Belajeff, that in the male gametophyte there are two antheridia, and not a single one as the present writer has held. The antheridium of the Schizæaceæ [1] [2] is relatively simple in structure, and might very well be compared to each of the groups of sperm-cells in Marsilia, with its two peripheral cells.

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[1] Bauke — Berträge zur keimungsgeschichte der Schizæaceæ *Prings. Jahrb.* XI, 1878.

[2] Britton, E. G. & Taylor,—A life history of Schizæa pusilla, *Bull. Torrey Bot. Club*, XXVIII, 1901.

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